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A floristic-ecological classification of the shrublands of the dry Bolivian Altiplano

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Abstract

Aims: To identify shrubland types of the Bolivian Altiplano based on their floristic composition and on ecological factors. Location: Central and southern Bolivian Altiplano (Bolivia, central-western South America). **Methods:** Vascular plants were recorded in a field survey of 101 relevés (10 m²). Relevés were subjected to hierarchical agglomerative classification to define numerical vegetation groups. Classification techniques were based on the β-flexible linkage method (β = -0.25) with Sørensen distance. The highest crispness values defined the level of the main number of clusters identified. Diagnostic species were identified by means of the phi coefficient of fidelity. Canonical Correspondence Analysis, the Kruskal-Wallis test and a Z test were performed to assess the key ecological drivers of diversity in the Altiplano shrubland vegetation. **Results:** Based on numerical analyses of phytosociological relevés, our work proposes four vegetation types of shrublands in the dry central and southern Bolivian Altiplano. They correspond to the following: tolillares – thickets of *Fabiana densa* – of the central-southern Altiplano with *Junellia seriphioides*; tolillares of the central-northern Altiplano with *Lobivia pentlandii*; lampayares – thickets of *Lampayo castellani* – with *Parastrephia quadrangularis*; and tolares – thickets of *Parastrephia* sp. pl. – with *Parastrephia lepidophylla* and *Junellia minima*. The bioclimatic variables were the ones best explaining the distribution patterns of the shrubland vegetation in the dry Bolivian Altiplano. Specifically, they separate the tolillares of the central-northern Altiplano with *Lobivia pentlandii* – at localities with a higher annual precipitation, annual ombrothermic index, and ombrothermic index of the wettest quarter – from the tolillares of the central-southern Altiplano with *Junellia seriphioides*. These bioclimatic gradients also position lampayares at localities with a lower than average value of annual precipitation, annual ombrothermic index, and ombrothermic index of the wettest quarter. Significant differences were found when comparing the topographic position, the degree of soil drainage and the frequency of flooding between the vegetation of tolillares on the one hand, and the vegetation of lampayares and tolares, on the other. Lampayares were exclusively related to sandy soils. **Conclusions:** Our four groups characterize variation within the habitat and elucidate bioclimatic gradients and soil features with related habitats. This knowledge could provide basic information on the vulnerability of different Altiplano shrubland habitats to climatic fluctuations, as this area is highly vulnerable to extreme periods of drought associated with the regional effects of climate change as well as to anthropogenic factors.

Keywords: Andean region; diagnostic species; *Fabiana densa*; *Lampayo castellani*; *Lobivio ferocis-Fabianion densae*; numerical classification; orotropical climate; *Parastrephia lepidophylla*; *Parastrephion lepidophyllae*; plant-community type; shrubland.

Taxonomic reference: Bolivia Catalogue (2014; http://www.tropicos.org/Project/BC).

Syntaxonomic reference: Navarro (1993, 2002, 2011).

Abbreviations: CCA = Canonical correspondence analysis; Io = annual ombrothermic index; Iod = ombrothermic index of the driest quarter; Iow = ombrothermic index of the wettest quarter; Tw = mean temperature of the wettest quarter.

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Introduction

The Bolivian Altiplano is, after the Tibetan plateau, the largest and highest plateau in the world. It belongs to the Central Andean Dry Puna ecoregion, a very dry high-elevation montane territory whose flora and fauna are highly adapted to this extreme environment (Olson & Dinerstein 1998). The Bolivian Altiplano corresponds to the Altiplanean biogeographic province, where plant genera such as *Lampayo* (*Verbenaceae*), *Parastrephia* (*Asteraceae*) and *Fabiana* (*Solanaceae*) have their centre of diversity and form the core of the shrubland plant communities, the main vegetation matrix in the Bolivian Altiplano (Navarro 1993, 2002, 2011). Our study focused on these formations, which constitute the natural potential vegetation in large areas with dry and semi-arid climates, and are also affected by strong thermal inversions in the dry season. They form part of the seral vegetation of *Polylepis* woodlands only on mountainous slopes in mountain ranges in the eastern and western Altiplano, with a more humid climate and an absence of very intense frost in peripheral mountains (Navarro et al. 2005). The absence of *Polylepis* forest in the Altiplanic plain might be due to the bad drainage and salinity of the soils, as well as to the strong thermal inversions to which these areas are subjected.

Central Andean shrublands have been widely studied in Argentina (Fries 1905; Cabrera 1957, 1971, 1994; Ruthsatz 1977; Martínez Carretero 1995). In Bolivia, some types of Altiplanean shrubland have been phytosociologically studied by Navarro (1993, 2002, 2011). They have also been described in a general or applied form, for example in relation to livestock, firewood or their medicinal value (Lara & Alzérreca 1982; Beck 1985; Ibisch et al. 2003; García & Beck 2006, among others). Nevertheless, there is still a need for an updated floristic-ecological classification of Andean shrubland communities. This basic knowledge is particularly important for any environmental management in the Altiplano, and particularly in the Bolivian territory which is more sensitive and vulnerable to climate change (Rigoberto et al. 2007), and where the specific forecast is for a sharp rise in the mean annual temperature and a greater rainfall deficit.

The main aim of this work is to provide a comprehensive overview of the floristic-ecological diversity of the shrublands in the dry Bolivian Altiplano. Our study is based on our own original floristic relevés collected on these shrublands. The specific aims of this work are: (1) to organize floristic relevés into discrete floristic groups and define their diagnostic species; and (2) to determine the floristic relationships between these groups and the major environmental gradients that best explain the variability of the floristic composition.

Study site

The Altiplano or Andean plateau, extending from SW Peru over W Bolivia to NE Chile and NW Argentina, reaches its greatest extension in Bolivia, where it has an average width of 150–220 km and elevation of c. 3700 m a.s.l. The greatest width (220 km) is found around latitude 18º30' S in Oruro and Poopó Lake. Between the hills, mountain ranges and plains of the Altiplano there are ample detrital glacis (gentle pediment slope cut across bedrock in drylands) that connect, in this case, the mountainous slopes with extensive saline depressions containing large lakes and salt flats. The lithology of the Altiplano plain is predominantly composed of fine Quaternary sediments (silt, clay and fine sands) with a fluvial-lacustrine origin, and extensive windswept areas that may form fields of sand dunes that locally attain considerable extensions. In contrast, the various mountain ranges and numerous hills interspersed in the plains of the Altiplano are formed from Paleozoic (shales, slates, sandstones) and Tertiary (sandstones, conglomerates) rocky materials (GEOBOL 1994; Suárez-Soruco 2000).

Calcareous areas can occasionally be found surrounding several areas of the Altiplano salt flats, somewhat raised above their present level. They correspond to karstified lacustrine algal terraces originating in the ancient large lakes that covered much of the central Altiplano region in the interglacial periods of the Pleistocene-Holocene era, from around 30,000 years b.p. (Minchin and Tauca Quaternary lacustrine phases). These calcareous lacustrine terraces mark the level reached by the waters of these paleolakes (Argollo 1994; Sánchez-Saldías & Fariña 2014; Chepstow-Lusty et al. 2005).

The Bolivian Altiplano has a cold, dry, predominantly high-mountain tropical climate, with high insolation and evapotranspiration, and strong winds almost all year round. Mean annual temperatures (T) generally range from around 5 ºC to 9 ºC (Vicente-Serrano et al. 2016). Average minimum temperatures in the coldest month of the year (June or July) range from –3 ºC to –12 ºC. Rainfall varies from approximately 400–500 mm/year in the north and east to 120–280 mm/year in the south and west. There is a high interannual variability in rainfall, with differences in total rainfall of between 80 and over 700 mm in dry and wet years. A characteristic climate phenomenon in the dry season (May to September) is the strong thermal inversion in several zones of the plateau, especially those located adjacent to or near the mountain ranges surrounding the Altiplano. According to Rivas-Martínez et al. (2011), the central Altiplano in Bolivia has a tropical dry xeric bioclimate, while the southern Altiplano has a tropical semi-arid xeric bioclimate.

In the Bolivian Altiplano, two major shrubland types are recognized: thickets of *Fabiana densa* known as tolillares and plant communities dominated by species of the genus *Parastrephia* (e.g. *Parastrephia lepidophylla*) known as tolares (Navarro 1993, 2002, 2011). Both the tolillares and tolares vegetation types are largely in geocatenal contact throughout the Bolivian Altiplano. On sandy dunes, the shrublands are characterized by *Lampayo castellani* and constitute the vegetation known as lampayares.

Material and methods

We compiled data from our own unpublished relevés (made from 1989 to 2016) corresponding to *tollillares*, *tolares* and *lampayares* on extensive xeric areas in the whole central and southern Bolivian Altiplano (Fig. 1). Sample plots were selected according to these physiognomic-ecological formations. Floristic data were recorded for each plot (10 m^2), and the cover of each species was estimated using the Braun-Blanquet (1979) scale. We also recorded soil features such as drainage, flooding, effervescence, salinity and texture. We used USDA (2017) classes to describe drainage, flooding frequency, effervescence and texture, and our own scale to describe salinity

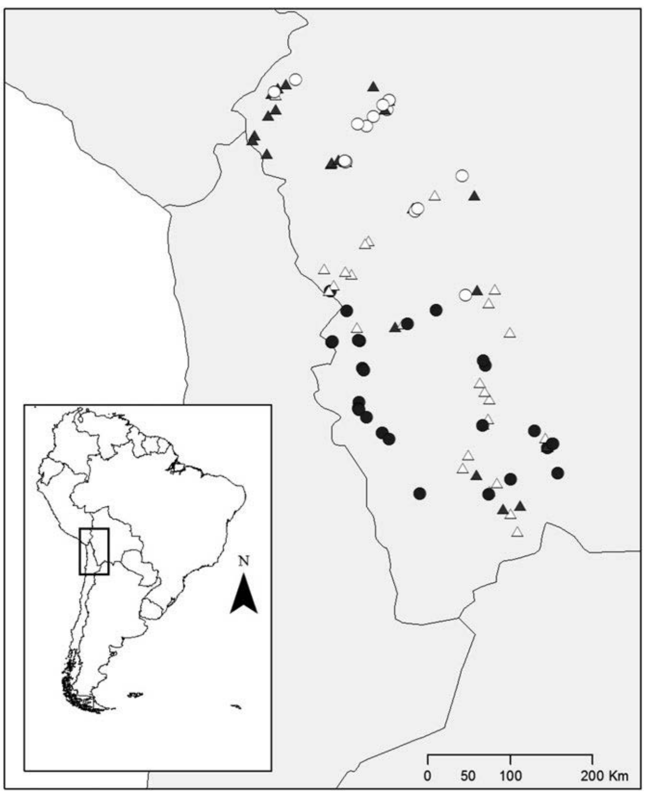

Fig. 1. Location of the study area (rectangle) showing the locations of the samples. Symbols correspond to groups in Table 1. *Tolillares* of the central-southern Altiplano (Group A), black circles; *tolillares* of the central-northern Altiplano (group B), white circles; *lampayares* (group C), white triangles; *tolares* (group D), black triangles.

(see footnote in Table 2). The position of the plot in the geocatena was documented according to the following scale: 1 = hill; 2 = high glacis; 3 = middle glacis; 4 = low glacis; and 5 = fluvio-lacustrine and alluvial plains.

The relevés were gathered, reviewed, and sorted in a table, which was subjected to analysis using numerical methods. Floristic data were revised, updated and corrected for any obvious misidentifications. The taxonomic nomenclature of the species follows the Bolivia Catalogue (2014; http://www.tropicos.org/Project/BC). An agglomerative classification method was first applied to the dataset using the β-flexible linkage method ($\beta = -0.25$) with Sørensen distance. Cover values were square-root transformed in order to reduce the importance of dominant species (Van der Maarel 1979). The crispness of the classification was checked using the method in Botta-Dukát et al. (2005). This method revealed the highest crispness at the level of two clusters (58.4) followed very closely at the level of four clusters (58.3), which was the option we chose since it explained four instead of two vegetation units in detail. A synoptic table was created with constancy values and diagnostic species. To define diagnostic species for each vegetation type, the phi coefficient of fidelity (Φ) was used (Chytrý et al. 2002). We show only the diagnostic species with values of the phi coefficient of association > 0.20 for at least one cluster, and with a statistically significant affinity at the probability level < 0.001 according to Fisher's exact test.

A Canonical Correspondence Analysis (CCA) was also performed to specifically assess the relationship between species composition and bioclimate. The following selected bioclimatic data were obtained from the WorldClim model (Fick & Hijmans 2017): total annual precipitation (P), mean annual temperature (T), mean temperature of the wettest quarter (Tw), mean temperature of the driest quarter (Td), precipitation of the wettest quarter (Pw) and precipitation of the driest quarter (Pd). The following calculated indexes are also included in the analysis: annual ombrothermic index (Io = P/T), ombrothermic index of the wettest quarter (Iow = Pw/Tw), and ombrothermic index of the driest quarter (Iod = Pd/Td). A Monte Carlo test was performed to determine the statistically significant environmental factors. Numerical analyses were done with the JUICE 7.0 (Tichý 2002) and CANOCO 4.5 programs (Microcomputer Power, Ithaca, NY, US). The Kruskal-Wallis test was used to compare differences in soil features (drainage, flooding, effervescence, and salinity) and topographic position (hill, glacis, fluvial terrace) among groups of vegetation resulting from the numerical classification (A–D). The Chi-square test and Z test with Bonferroni corrections were used to assess differences on textures among vegetation groups. Analyses were carried out using SPSS v.25 software.

Results

Classification and ordination analyses

The 101 relevés were arranged in four major groups (A, B, C and D) according to the crispness of the classification (Fig. 2, Table 1). Group A included 28 relevés and is characterized by a high constancy (> 75%) of *Fabiana densa* and *Junellia seriphioides*, which along with *Baccharis boliviensis* are the diagnostic species with the highest phi scores. Other species with high constancies in this group and also widespread in the Altiplano were *Baccharis tola* and *Adesmia spinosissima*. It is worth noting the species that are limited to group A, including *Chuquiraga atacamensis*, *Adesmia horrida*, *Atriplex imbricata*, *Fabiana squamata*, *Trichocereus atacamensis* and *Lophopappus cuneatus*. This group encompasses mainly *tolillares* shrublands distributed in the central-southern Altiplano (Fig. 1, Fig. 3A). Group B shows the northern Altiplanean endemic *Lobivia pentlandii* as the diagnostic species with the highest fidelity and high constancy values, in addition to other widely distributed Altiplanean species such as *Jarava ichu* and *Aristida asplundii* (Table 1). Other species with high constancy are *Baccharis tola*, *Cumulopuntia boliviana*, *Tetraglochin cristatum*, *Adesmia spinosissima* and *Fabiana densa*, among others. This group encompasses 15 relevés and includes *tolillares* mainly occurring in the central-northern Altiplano (Fig. 1, Fig. 3B). The diagnostic species with the highest fidelity and a high constancy in Group C were *Lampayo castellani* and *Parastrephia quadrangularis* (Table 1). *Parastrephia lepidophylla* also attains a high constancy. This group includes *lampayares* and it is found in central and southern Altiplano (Fig. 3C). Group D contains – like the previous group – 29 relevés and reveals *Junellia minima*, *Muhlenbergia fastigiata*, *Distichlis humilis* and *Parastrephia lucida* as diagnostic species with the highest fidelity scores (Table 1). It also has a high constancy of *Parastrephia lepidophylla*. This group includes the *tolares* found throughout the Altiplano (Fig. 1; Fig. 3D).

The CCA ordination (Fig. 4) applied to shrublands on the dry Bolivian Altiplano (Groups A, B, C and D) and nine bioclimatic variables showed that four of these features (P, Iow, Io and Tw) were significant ($p < 0.05$) in the Monte Carlo test. *Tolillares* vegetation was segregated in two groups (Group A and Group B) along axis 1, which in turn is highly correlated with P, Io and Iow. *Tolillares* in Group A (black circles) were mainly positioned in the left part of the diagram, so they can be inferred to be mainly characteristic of localities with lower than average values of P, Io and Iow. This group is centered on diagnostic species such as *Fabiana densa*, *Junellia seriphioides* and *Baccharis boliviensis*. The *tolillares* of the central-northern Altiplano are found in opposite positions (Group B, white circles), and are mostly located in the lower right quadrant of the diagrams in places with lower than average values of Tw. In these positions occur diagnostic species such as *Lobivia pentlandii*, *Jarava ichu* and *Aristida asplundii*. *Lampayares* shrublands (Group C, white triangles) are mostly grouped in the upper left quadrant in places with lower than average values of P, Io and Iow, and higher than average Tw. This group is centered on diagnostic species such as *Lampayo castellani* and *Parastrephia quadrangularis*. To complete the picture, *tolares* (Group D, black triangles) are mainly positioned in the right part of the diagram, centered on diagnostic species such as *Junellia minima*, *Muhlenbergia fastigiata* and *Distichlis humilis*.

Table 2 shows mean values and variance of ordinal edaphic variables in each vegetation group. No significant differences were found between group A and B nor between group C and D for any of the edaphic factors.

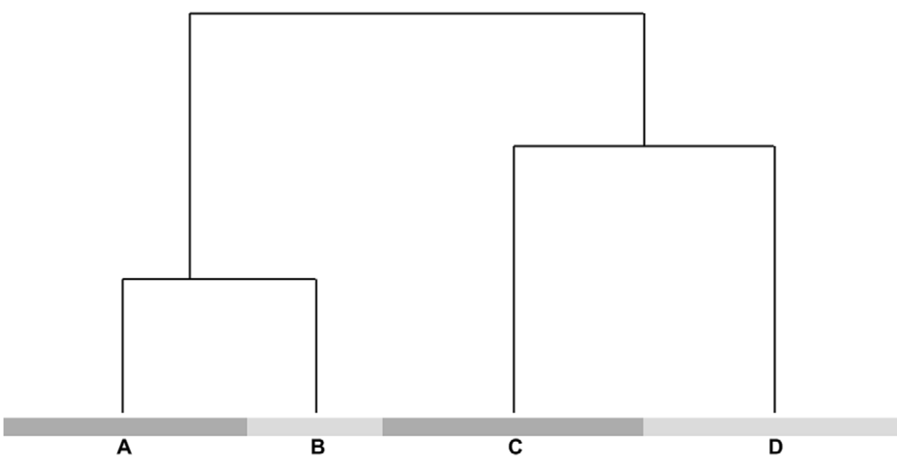

Fig. 2. Dendrogram of β-flexible clustering analysis applied to the shrublands of the dry Bolivian Altiplano data-set, with 101 relevés and 73 species. Cluster groups (A-D) correspond to those in the synoptic table (Table 1).

Table 1. Synoptic table of the shrublands of the dry Bolivian Altiplano showing the constancy values of species in each of the four vegetation units (columns) obtained in the classification analysis. Only species with a constancy > 25% in at least one group are included. Grey background colour indicates diagnostic species with phi coefficient > 0.20. Mean cover is indicated as superscript. E subscript after the name of the species means that it is an endemic plant to Bolivian Altiplano.

Higher-Level Cluster-Groups	**A**	**B**	**C**	**D**
Nº of relevés	**28**	**15**	**29**	**29**
Characteristic and Differential species				
High Andean shrublands (*Parastrephio lepidophyllae-Fabianetea densae*)				
Fabiana densa	100^{3}	60	28	7
Parastrephia quadrangularis	36	13	72^{2}	21
Baccharis tola	75	100	55	45
Parastrephia lepidophylla	7	73	93	86
Cumulopuntia boliviana	32	87	10	24
Frankenia triandra	25	27	66	48
Adesmia spinosissima	75	73	45	10
Ephedra rupestris	50	53	31	17
Festuca orthophylla	11	27	52	62
Nasella nardoides	21	7	48	34
Astragalus arequipensis	4	33	3	7
Jarava leptostachya	29	13	7	3
Tolillares communities (*Lobivio ferocis-Fabianion densae*)				
Junellia seriphioides	86^{2}	.	17	.
Baccharis boliviensis	64^{3}	13	14	.
Lobivia pentlandii	.	80^{1}	3	7
Cumulopuntia chichensis $_{E}$	39	7	3	3
Airampoa ayrampo	36	60	7	.
Senecio potosianus $_{E}$	32	13	3	.
Jarava plumulosa	21	.	7	3
Echinopsis longispina	43	7	.	.
Cherdosoma jodopappa	29	13	.	.
Nassella arcuata	25	20	.	.
Lycium chanar	29	.	3	.
Maihueniopsis nigrispina $_{E}$	25	.	7	.
Chuquiraga acanthophylla	25	.	3	.
Chuquiraga atacamensis	32	.	.	.
Adesmia horrida	29	.	.	.
Trichocereus atacamensis	29	.	.	.
Atriplex imbricata	25	.	.	.
Fabiana squamata	25	.	.	.
Lophopappus cuneatus	25	.	.	.
Portulaca perennis	.	27	.	.
Tolares and Lampayares communities (*Parastrephion lepidophyllae*)				
Lampayo castellani	7	.	66^{3}	3
Junellia minima	.	27	10	86^{2}
Muhlenbergia fastigiata	.	27	3	59^{2}
Distichlis humilis	.	7	10	34^{2}
Parastrephia lucida	.	.	21	45^{1}
Deyeuxia curvula	.	.	7	28

Table 1. cont.

Higher-Level Cluster-Groups	A	B	C	D
Nº of relevés	**28**	**15**	**29**	**29**
Widely distributed species				
Jarava ichu	29	100^{2}	14	41
Aristida asplundii	14	73^{2}	10	7
Tetraglochin cristatum	29	87	72	66
Bouteloua simplex	11	27	31	10
Muhlenbergia peruviana	.	27	7	7
Nassella meyeniana	.	33	3	17
Adesmia miraflorensis	7	53	.	.

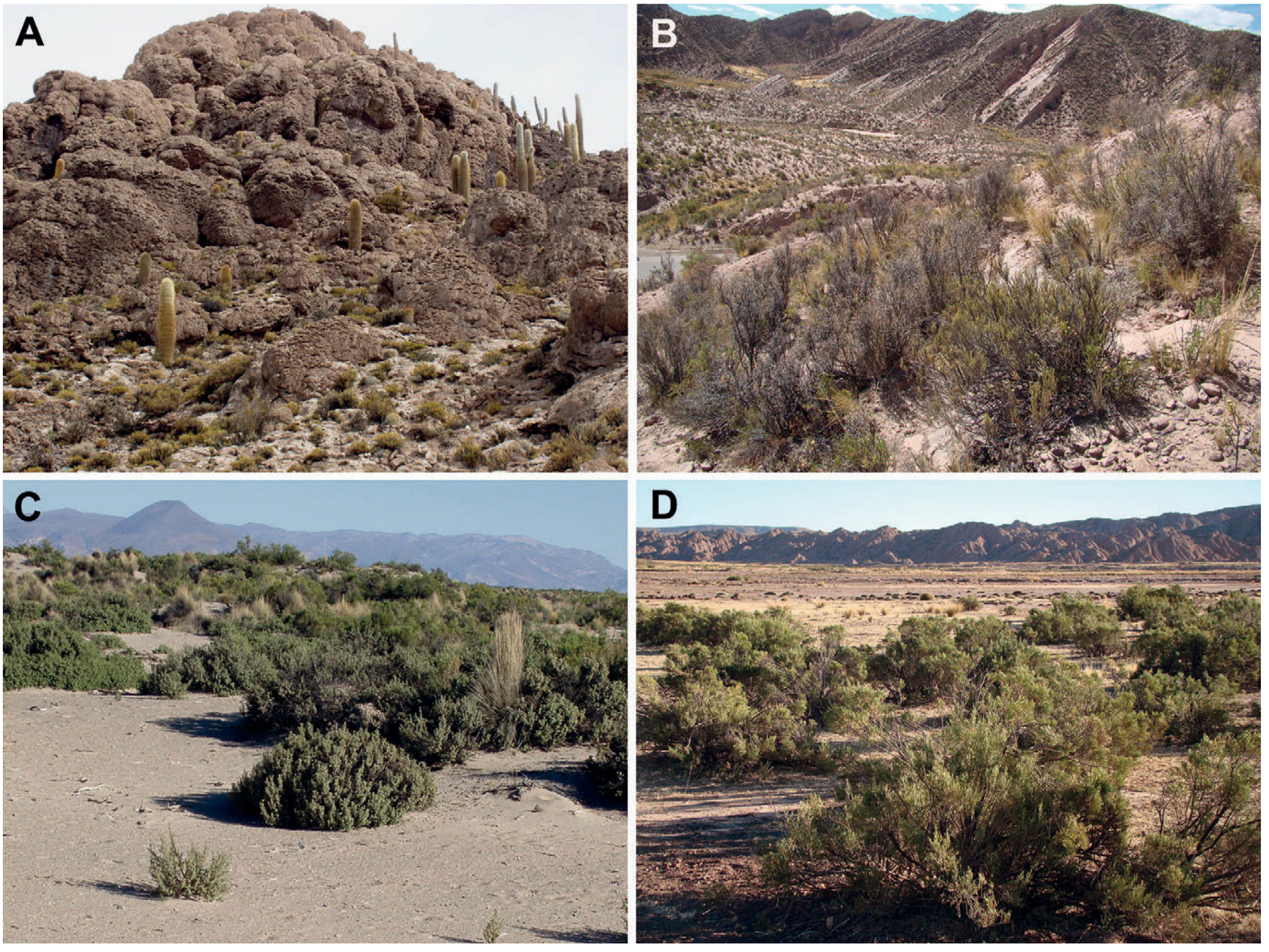

Fig. 3. Photographs showing the plant-landscape physiognomy of shrublands of the dry Bolivian Altiplano. **A.** *Tolillares* of the central-southern Altiplano with *Lycium chanar* and *Atriplex imbricata* (Group A) in margins of the north of Salar de Coipasa, between Sabaya and Coipasa (Oruro). **B.** *Tolillares* of the central-northern Altiplano with *Lobivia pentlandii* and *Parastrephia lepidophylla* (Group B), between Umala and Desaguadero River (Departmento de La Paz). **C.** *Lampayares* of *Lampayo castellani* with *Parastrephia quadrangularis* (Group C) in sand dunes in the west of the Altiplano (Oruro: Sabaya to Todos Santos). **D.** *Tolares* with *Parastrephia lepidophylla* and *Frankenia triandra* (Group D) in Calacoto (Departamento de La Paz).

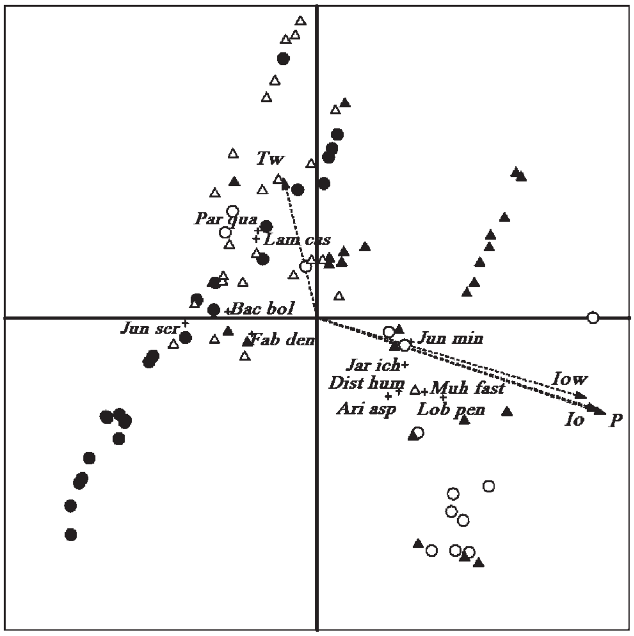

Fig. 4. Species-conditional biplot of the shrublands of the dry Bolivian Altiplano based on a CCA. Symbols correspond to those in Figure 1. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.40 and 0.19, respectively. The displayed environmental variables are those significant in the Monte Carlo test. P= annual rainfall, Tw = mean temperature of the wettest quarter, Io= annual ombrothermic index Io = P/T), and Iow = ombrothermic index of the wettest quarter (Iow= Pw/Tw). Plant abbreviations of the diagnostic species are as follows: Ari asp, *Aristida asplundii*; Bac bol, *Baccharis boliviensis*; Dist hum, *Distichlis humilis*; Fab den, *Fabiana densa*; Jar ich, *Jarava ichu*; Jun min, *Junellia minima*; Jun ser, *Junellia seriphioides*; Lam cas, *Lampayo castellani*; Lob pen, *Lobivia pentlandii*; Muh fast, *Muhlenbergia fastigiata*; Par qua, *Parastrephia quadrangularis*.

However, significant relationships were found when comparing the overall *tolillares* vegetation (groups A and B) with that formed by *lampayares* and *tolares* (groups C and D) in terms of topography, soil flooding and soil drainage (Kruskal-Wallis test, $p < 0.001$). *Tolillares* occur on better-drainage and less-flooded soils than *lampayares* and *tolares*. Topographically, *tolillares* occupy mostly mountain slopes and high glacis, whereas *tolares* and *lampayares* are mostly found in alluvial plain and low glacis. The cross tabulation resulting from Z test showed a significant relationship between *lampayares* (group C) and sandy texture soils (Table 3).

Discussion

Vegetation units

Vegetation is often regarded as a very good surrogate descriptor of habitats and ecosystems (Jennings et al. 2009). In the shrublands of the dry Bolivian Altiplano, agglomerative classification identified two vegetation units at the higher level (namely *tolillares* – Groups A and B –, *lampayares* – Group C – and *tolares* – Group D). These numerical results support the major vegetation units of *Lobivio ferocis-Fabianion densae* (Groups A and B) and *Parastrephion lepidophyllae* (Groups C and D), described as alliances by Navarro (1993). Along with the alliance *Diplostephio meyenii-Fabianion ramulosae* (Luebert & Gajardo 2000; Luebert & Gajardo 2005), they all constitute the synopsis of the shrubland vegetation of the dry Altiplano through SW Peru, W Bolivia, NE Chile and NW Argentina. These alliances are encompassed in the phytosociological class and order of *Parastrephio lepido-*

Table 2. Mean values and variance of the topographic position and edaphic variables in each of the 4 vegetation units (A-D) obtained from clustering analysis.

Higher-Level Cluster-Group	Group A		Group B		Group C		Group D	
Edaphic variables (range)	**Mean**	**Variance**	**Mean**	**Variance**	**Mean**	**Variance**	**Mean**	**Variance**
Topography (1-5)	1.36	0.386	1.33	0.667	3.59	1.894	3.66	2.948
Drainage (1-5)	1.75	0.491	2.20	0.886	2.62	1.744	3.55	1.685
Flooding (0-5)	0.07	0.069	0.13	0.124	0.97	1.963	1.76	2.833
Effervescence (1-5)	2.07	1.772	1.87	0.981	2.17	1.291	2.10	1.239
Salinity (0-5)	0.39	0.396	0.40	0.257	0.69	1.293	0.86	1.195

Topography class (1-5): 1 = Mountain slope; 2 = High glacis; 3 = Middle glacis; 4 = Low glacis; 5 = Fluvio-lacustrine and alluvial plains. **Drainage** class (USDA 2017): 5 = Very poorly drained; 4 = Somewhat poorly drained to poorly drained; 3 = Moderately well drained; 2 = Well drained; 1 = Excessively to somewhat excessively drained. **Flooding** frequency class (USDA 2017): 0 = None; 1 = Very rare; 2 = Rare; 3 = Occasional; 4 = Frequent; 5 = Very frequent. **Effervescence** class (USDA 2017): 1 = Non effervescent; 2 = Very slightly effervescent; 3 = Slightly effervescent; 4 = Strongly effervescent; 5 = Violently effervescent. **Salinity** class: 0 = total absence of efflorescence; 1 = very thin or patchy efflorescence 2 = thin and discontinuous salt crust; 3 = Thin salt crust unevenly spread over the surface of the soil; 4 = moderately coarser almost continuous crust; 5 = medium thick continuous surface crust.

Table 3. Contingency table for soil texture classes and vegetation groups.

Higher-Level Cluster-Group		Group A	Group B	Group C	Group D
Texture 1	Count	0_a	1_a	0_a	5_a
	%	0.0%	6.7%	0.0%	17.2%
Texture 2	Count	1_a	3_a	7_a	7_a
	%	3.6%	20.0%	24.1%	24.1%
Texture 3	Count	$6_{a, b}$	$4_{a, b}$	1_b	11_a
	%	21.4%	26.7%	3.4%	37.9%
Texture 4	Count	21_a	$7_{a, b}$	9_b	6_b
	%	75.0%	46.7%	31.0%	20.7%
Texture 5	Count	0_a	0_a	12_b	0_a
	%	0.0%	0.0%	41.4%	0.0%
Total	Count	28	15	29	29
	%	100.0%	100.0%	100.0%	100.0%

Texture class (1-5): 1 = clayey; 2 = silty; 3 = loam; 4 = loam-sandy; 5 = sandy

phyllae-Fabianetea densae and *Parastrephietalia lepidophyllae*, respectively (Navarro 2002).

A subsequent step in our cluster analysis split the vegetation matrix into the four groups defined in the results (A, B, C, D), in which diagnostic species were identified in each group, mostly with high constancy (Table 1). They can therefore be identified as subunits – maybe sub-alliances – each containing one or more associations or community types that have been described previously (Navarro 1993) or have yet to be described. These subunits, which are named in relation to dominant and diagnostic species, correspond to the following: *tolillares* – thickets of *Fabiana densa* – of the central-southern Altiplano with *Fabiana densa* and *Junellia seriphioides* (Group A), *tolillares* of the central-northern Altiplano with *Lobivia pentlandii* (Group B), *lampayares* of *Lampayo castellani* with *Parastrephia quadrangularis* (Group C), and *tolares* with *Parastrephia lepidophylla* and *Junellia minima* (Group D). Phytosociological associations already described in the Bolivian Altiplano are the *Lobivio pentlandii-Fabianetum densae* and *Gutierrezio gillesii-Verbenetum seriphioidis* within the *Lobivio ferocis-Fabianion densae* alliance; and the *Muhlenbergio fastigiatae-Parastrephietum lepidophyllae* and *Acantholippio hastulatae-Lampayoetum castellani* within the *Parastrephion lepidophyllae* alliance (Navarro 1993).

Ecological patterns and habitat conservation

Both climate and soil have been identified as major drivers in montane shrubland distribution around the world (e.g. Li et al. 2016). Our study focuses on the shrublands of the dry Bolivian Altiplano and reveals bioclimatic factors as being the most important variables differentiating floristic composition. Specifically, annual precipitation, annual ombrothermic index and ombrothermic index of the wettest quarter clearly distinguished the distribution of the *tolillares* groups, positioning the *tolillares* of *Lobivia pentlandii* in less dry areas. Besides, *lampayares* were associated to drier and warmer areas in which the climatic conditions favor the movement and deposit of the sand to which the *lampayares* is related. The ombrothermic index (Io) has been observed to be an important factor to distinguish other wooded habitat types in the high Andes, such as the Bolivian *Polylepis* forest (Navarro et al. 2005).

Our study also related soil factors to vegetation types. In particular, *tolillares* are chiefly found in hillsides on well-drainage soils and little or none prone to flooding. On the other hand, *lampayares* and *tolares* occur in low glacis and plains on soils with poorer drainage and more susceptible to flooding. Statistical analyses also revealed that *lampayares* are closely related to sandy soils. These findings support previous observational hypotheses (Navarro 1993, 2002) about the ecology of the dry Altiplanean shrublands, which linked *tolillares* to coarse-textured non-flooded soils, *lampayares* to windswept surfaces and sand dunes and *tolares* to fine-textured substrates that are poorly drained or subject to flooding. In light of all this, the *tolillares* constitute zonal vegetation in equilibrium with the climate, which makes possible a spatial segregation between the northern *tolillares* – in areas with more humid climate – and the southern ones – in areas with drier climate. Meanwhile, *tolares* and *lampayares* correspond to azonal (soil-dependent) vegetation, being therefore distributed in favourable substrates throughout the Altiplano.

The projected climate changes in tropical South America at the end of the 21st century are dominated by a significant warming and by a general decrease in winter (June-August) precipitation (Urrutia & Vuille 2009). Future climate change will lead not only to an upslope but also to a downslope expansion for the dry Andean biomes (Tovar et al. 2013). In the coming scenario of higher temperatures and lower rainfall, the habitats related to the northern and relatively more humid *tolillares* with *Lobivia pentlandii* are probably the most threatened due to their connection to wetter climates. On the other hand, the *tolillares* are considered xerophytic vegetation while the *tolares* are considered phreatophytic vegetation. The projected decrease in rainfall in the Altiplano area will have an impact on the recharge of the aquifers on which the *tolares* depend. The monitoring of the extension of the *tolillares* versus the *tolares* can be a good indicator of climate change. Moreover, the monitoring of the extension and state of health of the *tolares* (excluding their extraction as firewood) can be an indicator of the recharge and condition of the aquifers. These potential changes might be recognized and serve for ecosystem monitoring over coming decades.

No assessments of habitat conservation have been made in Bolivia, unlike in other parts of the world (Janssen et al. 2016). The vegetation of the *tolares* is highly susceptible to various predominantly anthropogenic factors such as overgrazing, excessive exploitation for firewood, and clearing to grow quinoa (VMMAyA 2012). The *tola* (*Parastrephia lepidophylla*) is itself considered threatened due to its overexploitation for firewood (Navarro et al. 2012a; VMMAyA 2012), while *tolillares* shrublands serve as a habitat for endangered species including several Altiplano cacti such as *Trichocereus tarijensis*, which is considered vulnerable (Navarro & De la Barra 2012). Other important species in the dry Bolivian Altiplano plant landscape are also endangered, as are the cases of *Parastrephia quadrangularis* and *Lampayo castellani* which are considered vulnerable (Navarro et al. 2012b, 2012c).

Author contributions

G.N. planned the research, conducted the field sampling and identified the plant species, J.A.M. performed the statistical analyses, and both authors participated in discussion of the results and the writing of the manuscript.

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